

# Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests

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Numerical superiority confers a competitive advantage during contests among animal groups, shaping patterns of resource access, and, by extension, fitness. However, relative group size does not always determine the winner of intergroup contests. Smaller, presumably weaker social groups often defeat their larger neighbors, but how and when they are able to do so remains poorly understood. Models of competition between individuals suggest that location may influence contest outcome. However, because of the logistical difficulties of studying intergroup interactions, previous studies have been unable to determine how contest location and group size interact to shape relationships among groups. We address this question by using an automated radio telemetry system to study intergroup interactions among six capuchin monkey (*Cebus capucinus*) social groups of varying sizes. We find that the odds of winning increase with relative group size; one additional group member increases the odds of winning an interaction by 10%. However, this effect is not uniform across space; with each 100 m that a group moves away from the center of its home range, its odds of winning an interaction decrease by 31%. We demonstrate that contest outcome depends on an interaction between group size and location, such that small groups can defeat much larger groups near the center of their home range. The tendency of resident groups to win contests may help explain how small groups persist in areas with intense intergroup competition.

between-group competition | intergroup dominance | payoff asymmetries | resource holding potential

In social species ranging from ants to humans (1, 2), groups compete over access to resources, such as food (3–5), mates (6), and water (7), that are critical for survival and reproduction. Competitive ability increases with group size in many species (1, 2, 8–13), and this trend is thought to provide a selective pressure favoring group living (14–17). Numerical superiority, however, does not ensure victory (3, 18–21). Even in species where group size strongly predicts the outcome of intergroup contests, small groups are frequently victorious (3). When and how groups are able to overcome a numerical disadvantage are critical factors determining the costs and benefits of grouping, but remain poorly understood.

Theoretical work on contests between individuals provides a useful framework for thinking about contests among groups. Models of competition between individuals suggest that contest outcome depends on two fundamental factors (22). First, asymmetries in fighting ability [resource holding potential (RHP)] may reliably predict which individual prevails (23). Second, asymmetries in payoff (the consequences of winning or losing an interaction) may affect the intensity with which contestants compete. Location-based payoff asymmetries arise if residents place a higher value on the area being contested than intruders, and thus have more to gain from winning the interaction (or more to lose in defeat) (22, 24). Home range centers, for example, might be more valuable than peripheral areas if ranges

are established in areas of particularly high resource density, if knowledge gained through frequent use of an area creates foraging advantages (25), or if competition with neighbors decreases foraging efficiency in peripheral areas (26, 27). For similar reasons, frequently used areas might be highly valued regardless of their position in the home range.

Intergroup competition is more complex than interindividual competition because it depends on the actions of multiple independent participants. For example, group size likely determines the maximum RHP of a group, but the number of individuals who decide to participate in any given interaction determines the realized RHP. Nonetheless, it is likely that the same factors that are important in contests between individuals also influence the outcome of contests among groups.

Despite its role in shaping access to resources, few studies have investigated which factors predict success in intergroup competition (but see refs. 28–30), and none has investigated how group size and contest location interact to determine the outcome of competitive interactions. This topic has been neglected in part because intergroup contests are relatively infrequent, making it difficult to obtain a sufficient sample size to distinguish between competing hypotheses. The logistical difficulties of simultaneously following multiple social groups also make such studies expensive and time consuming. Finally, differences in habituation level across study groups are a concern when traditional observation techniques are used to investigate intergroup competition because the presence of an observer may influence contest outcome. The behavioral reaction of less habituated groups to the observer may negatively impact their chances of winning an interaction and artificially inflate the competitive success of well habituated groups.

We overcame these challenges by using an Automated Radio Telemetry System (ARTS) to simultaneously monitor the movements of six white-faced capuchin (*Cebus capucinus*; hereafter capuchin) social groups on Barro Colorado Island, Panama, from November 2004 to April 2005. ARTS enabled us to detect many more intergroup interactions than traditional techniques would have yielded in an equivalent period (see Table 1). It also provided a quantitative and unbiased method for identifying and determining the outcome of interactions by using spatial criteria. By using ARTS, we are able to address a long-standing question regarding intergroup relationships that had proved intractable with traditional data-collection methods.

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**Table 1. Summary of data collection for the six social groups**

Group	No. of adults	Animal ID	Sex	No. of locations	Data-collection period
TB	6	51	F	10,638	11/04–04/05
		87	F	4,147	03/05–04/05
BLT	5	52	M	8,515	11/04–04/05
		53	F	9,665	11/04–04/05
Top	10	54	F	8,000	11/04–04/05
		55	M	10,653	11/04–04/05
BL12	13	57	F	7,871	11/04–04/05
		58	M	7,437	11/04–04/05
FC	10	83	F	1,667	03/05–04/05
		84	F	1,662	03/05–04/05
Conrad	10	85	F	2,242	03/05–04/05
		86	F	2,073	03/05–04/05

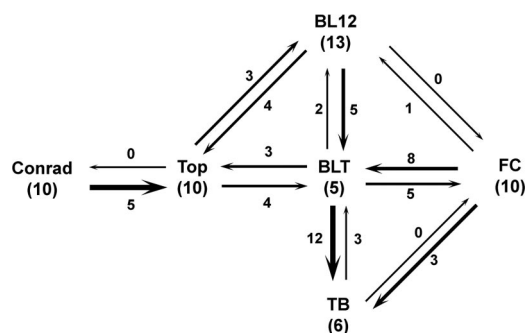
Animal ID is the individual identifier of radio-collared animals, no. of locations is number of location estimates recorded by ARTS, and data-collection period refers to the time period when ARTS data were collected for each individual.

Intergroup competition in capuchins is intense and occasionally lethal (31). Although group size is highly variable (32), previous research has shown that large groups do not necessarily defeat small groups (19). However, the effect of contest location on the outcome of intergroup encounters has not been assessed, and the relationship between group size and contest location has never been explored. Here we investigate the effects of group size, which is thought to determine a group's maximum RHP (33–35), and measures of location, which may create payoff asymmetries (36, 37), on the outcome of competitive intergroup encounters among capuchin social groups. Because males play a more prominent role in intergroup contests than females in this species (19, 38), and may therefore contribute more to the RHP of a group, we also investigate the importance of the relative number of adults of each sex in the group.

## Results

We identified 58 intergroup interactions in which one social group spatially displaced another (Fig. 1; see *Materials and Methods* for criteria used to define a displacement). Clear dominance relationships were only observed in two of eight group dyads. Relations between some groups were strongly one sided (BLT defeated TB in 12 of 15 interactions), but others were more evenly matched (BLT defeated FC in 5 of 13 interactions).

Large relative group size (focal group size minus opposing group size) conferred a competitive advantage. The odds of



**Fig. 1.** Summary of 58 intergroup interactions among the six social groups. Numbers in parentheses indicate the number of adult monkeys per group. Arrows point from winner to loser. Relative arrow thickness and associated numbers indicate sample sizes. For example, BL12 (13 individuals) defeated BLT (5 individuals) five times, and BLT defeated BL12 twice.

**Table 2. Output from a GEE multiple regression of focal group–intergroup interaction success probability versus relative group size (focal group size minus opposing group size) and location (distance from focal group's home range center in meters)**

Variable	Parameter estimate	Standard error	$\chi^2_1$	P
Intercept	1.56	0.63	6.2	0.01
Relative group size	−0.07	0.07	1.2	0.28
Location	−0.39	0.18	4.6	0.03
Group size by location	0.05	0.02	4.0	0.05

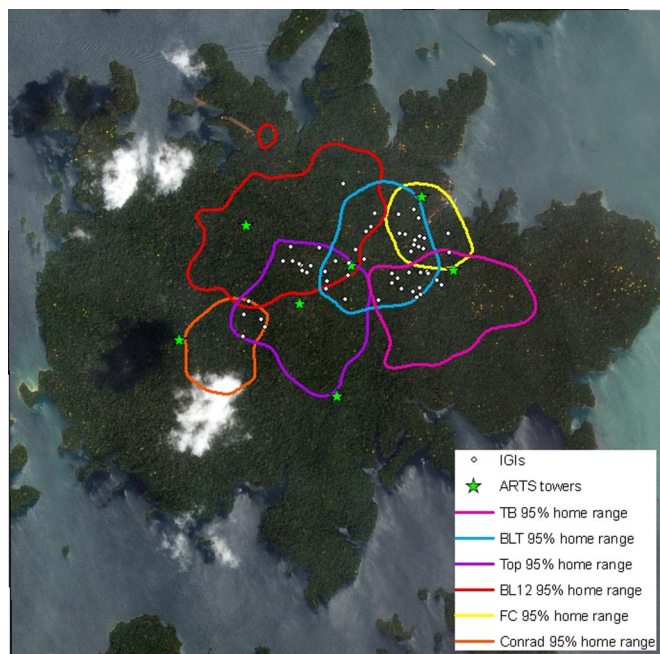
winning increased by 10% with each one-individual increase in relative group size [Generalized Estimating Equations (GEE) logistic regression, odds ratio: 1.10,  $\chi^2_1 = 11.8$ ,  $P = 0.0006$ , repeated measure = dyad]. Given that male capuchins are typically more consistent and aggressive participants in intergroup conflicts (19, 38), we explored the effect of the relative number of members of each sex on the likelihood of winning an interaction. Groups with relatively more males were more likely to win (GEE logistic regression, odds ratio: 1.68,  $\chi^2_1 = 24.6$ ,  $P < 0.0001$ , repeated measure = dyad), as were those with relatively more females (GEE logistic regression, odds ratio: 1.13,  $\chi^2_1 = 7.6$ ,  $P = 0.006$ , repeated measure = dyad). Because the number of males and females in a group were highly correlated ( $R^2 = 0.95$ ,  $P < 0.001$ ), we were unable to use multiple regression to determine whether the relative group size effect was driven by one sex or the other.

Although relatively larger groups were significantly more likely to win interactions, they did not always do so. For example, BLT won almost half of its interactions with Top, which had twice as many adults (Fig. 1). Additionally, the tendency to win was not transitive; although BL12 consistently beat BLT and BLT and Top were evenly matched, BL12 did not consistently beat Top. These results indicate that factors other than relative group size also influenced interaction outcome.

Indeed, as predicted, interaction location played an important role in determining the victor. Groups were more likely to win interactions close to the center of their home range. For every 100-m increase in distance from the center of its home range, a group's odds of winning decreased by 31% (GEE logistic regression, odds ratio: 0.69,  $\chi^2_1 = 8.5$ ,  $P = 0.0036$ , repeated measure = dyad). For example, on both occasions when BLT (5 adults) defeated BL12 (13 adults), the interaction took place relatively close to the center of BLT's home range (175 and 325 m, respectively). However, the degree to which the focal group had used the contested area in the 2 weeks before the interaction did not affect the interaction outcome (GEE logistic regression,  $\chi^2_1 = 0.34$ ,  $P = 0.56$ , repeated measure = dyad) even when controlling for relative group size ( $\chi^2_1 = 0.53$ ,  $P = 0.51$ ). These results suggest that geometric location within the home range, but not the intensity of use, tempers the effect of group size.

To more fully test this idea, we used a saturated GEE multiple logistic regression model (repeated measure = dyad) to examine the relationship among relative group size, location, and the probability of winning an interaction. Location (distance from the focal group's home range center) and the two-way interaction term (location by relative group size) were both statistically significant predictors of victory (Table 2). To aid in interpreting these results, we used the model parameters to predict the probability of winning for all combinations of relative group size and location (Fig. 2). All groups, regardless of size, were highly likely to win interactions that occurred close to the center of their home range. With increasing distance from the center of a group's home range, the probability of winning an intergroup





**Fig. 3.** Home ranges of the six study groups and locations of the intergroup interactions and the ARTS towers.

wide range of group sizes typically observed in a population to be maintained.

## Materials and Methods

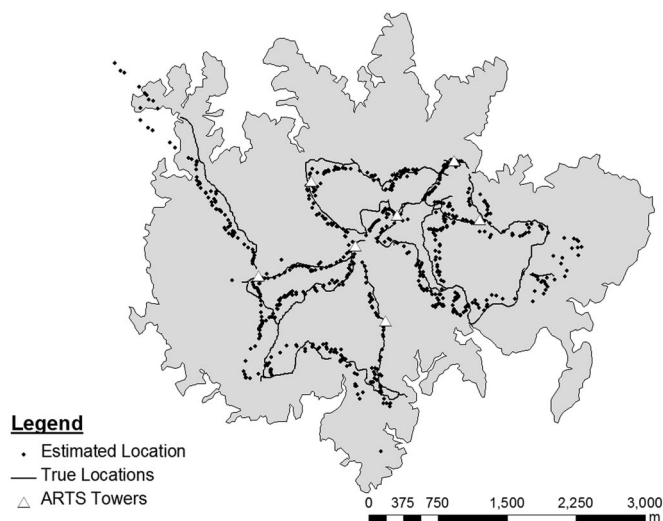
We studied six groups of white-faced capuchin monkeys between June 2004 and September 2005 at the Smithsonian Tropical Research Institute on Barro Colorado Island, Panama (see Fig. 3). The research described here received clearance from the Harvard University Institutional Animal Care and Use Committee (assurance no. A-3593-1).

**Automated Radio Telemetry.** We captured two monkeys in each social group, fitted them with radio collars, and used ARTS to monitor their movement. ARTS is a multiuser infrastructure that provides researchers with the ability to continuously and simultaneously monitor the location of a large number of radio-collared animals. The automated receivers were designed by Cochran (47) and were deployed into the tracking system by the ARTS Initiative (<http://160.111.238.241/%7Ecocoss/index.php>). For a detailed description of the automated receiving units, see Larkin *et al.* (48).

The system consisted of seven 40-m steel towers each topped with a fixed array of six directional antennas and each connected to an automated receiving unit (see Fig. 3). The automated receivers were synchronized to scan through a list of radio frequencies corresponding to the specific transmitters being worn by study animals. They recorded the relative strength of the radio signals across the fixed antenna arrays and transmitted these data in real time via a wireless network (FreeWave; [www.freewave.com](http://www.freewave.com)) to a server at the Smithsonian Tropical Research Institute on Barro Colorado Island, where they were automatically loaded into a web-accessible PostgreSQL database. The relative signal strengths were converted into bearings within the database, and these bearings were smoothed by using signal-processing software (PV-Wave; Visual Numerics) to reduce noise. The system recorded one bearing every 1.5 s and took 10 bearings for each frequency before continuing to the next frequency on the search list. These 10 bearing estimates were then used to triangulate a single location estimate.

We conducted test walks to measure the locational error of the ARTS system by carrying a radio collar along trails that had been georeferenced with a global positioning system at 100-m intervals. Location estimates produced by ARTS were then compared with the true locations to measure system error. ARTS accuracy varied depending on the location of the transmitter. Error was smallest in central portions of the island and largest toward the periphery (range 39–166 m) (see Fig. 4). The average error within the home ranges of the study groups was 42 m (SD = 34).

In this study, the location of each subject was recorded every 10 min for a



**Fig. 4.** Results of the test walk conducted to assess ARTS accuracy. Error was <50 m in the central portions of the island where this study was conducted.

period of 2–6 months (see Table 1). We triangulated locations from the smoothed bearings by using an Andrew's M estimator (49, 501) implemented in the software program LOAS ver. 4.0 (51). Data visualization and analysis were conducted by using the software packages ArcGIS (ESRI) and Biotas ver. 1.03 alpha (52).

**Analyses.** We used two spatial criteria to identify intergroup interactions: (i) two groups approached to within 150 m of one another, and (ii) one group remained at the site of the interaction for at least 20 min after the other group left the site of the interaction [see [supporting information \(SI\) Movie 1](#)]. The group that remained at the site of the encounter won the interaction, whereas the group that left lost. These definitions were based on 23 intergroup interactions observed during behavioral sampling (six 3-h follows per group per month conducted by M.C.C.) between November 2004 and September 2005 and are consistent with previous behavioral studies of intergroup interactions in primates (29, 53).

Although female capuchins participated, at least occasionally, in intergroup agonism in all populations where the relevant data were available (19, 38, 39, 54, 55), adult males played a more prominent and regular role (19, 38, 39, 56, 57). In many intergroup contests, females quickly and quietly left the site of the conflict, whereas males rushed forward and engaged in displays, chases, and occasionally contact aggression (19, 38). For this reason, we tested whether the sex of radio-collared individuals in a group influenced the likelihood of the group winning an interaction by the criteria described in the previous paragraph. Half the groups had one individual of each sex radio-collared, whereas the other groups contained two radio-collared females. There was no effect of the sex of the collared individuals on the probability that the focal group won (GEE logistic regression,  $\chi^2_1 = 0.18$ ,  $P = 0.67$ ).

Home range size tended to increase with group size (38). We defined the center of each group's home range as the average  $x$  and  $y$  coordinates of all the locations of the collared individuals in a given group over the course of the entire study period. To assess the intensity with which various parts of the range were used, we overlaid a  $50 \times 50$ -m grid on the study area. For the 2-week period preceding each intergroup encounter, we calculated the number of observations in each grid cell as a percentage of the total number of observations. We used the percentage of observations in the grid cell where the encounter occurred as our measure of use. Group size was assessed by counting the number of adults present in each group at the beginning of each of the regular behavioral observations. The number of adults in each study group remained stable during the 6 months that comprised this portion of the study. However, both direct observation and ARTS monitoring revealed that the largest group (BL12; 13 adults) occasionally split into two subgroups during low-food-availability months (November–December 2004). For this reason, encounters involving BL12 during these months were not included in the study.

All hypotheses were tested by using logistic regression, and statistical analyses were performed with SAS version 9.1 (SAS Institute). We used GEE (58) to control for repeated interactions between the same group dyads. This

